

Fiber Architecture of the Extensors of the Hindlimb in Semiterrestrial and Arboreal Guenons

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ABSTRACT Fiber architecture of the extensor musculature of the knee and ankle is examined in two African guenon species—the semiterrestrial *Cercopithecus aethiops*, and the arboreal *C. ascanius*. Using histologic and microscopic techniques to measure lengths of sarcomeres, the original lengths of muscle fasciculi and angles of pinnation in quadriceps femoris and triceps surae are reconstructed from direct measurements on cadavers. Calculations of reduced physiological cross-sectional area, mass/predicted effective tetanic tension, maximum excursion, and tendon length/fasciculus + tendon lengths are correlated to preferred locomotor modalities in the wild.

For both species, greater morphological differences occur among the bellies of quadriceps femoris—rectus femoris, vastus intermedius, v. lateralis, and v. medialis—than among the bellies of triceps surae—gastrocnemius lateralis, g. medialis, plantaris, and soleus. With regard to quadriceps femoris, few differences occur between species. Interspecific differences in the triceps surae indicate (1) redirection of muscle force to accommodate arboreality in which the substrate is less than body width; (2) muscles more suited for velocity in the semiterrestrial vervets; and (3) muscles used more isotonicity in vervets and more isometrically in red-tailed monkeys. The inherent flexibility of muscle may be preadaptive to a primary species shift in locomotor modality until the bony morphology is able to adapt through natural selection.

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That skeletal conformation is linked to preferred locomotor modality has been demonstrated innumerable times in primates. However, complementary information regarding the “musculo-” moiety of the musculoskeletal system is much less frequently found. A few published studies are available, however, and consider biomechanical leverage based on relative muscle size and position in correlating the morphological results with information about naturalistic locomotor behavior (e.g., Ashton and Oxnard, 1963; Stern, 1971; Fleagle, 1977; Ward and Sussman, 1979). Although commonly found in the nonprimate mammalian (e.g., Gonyea and Ericson, 1977; Spector et

al., 1980; Sacks and Roy, 1982; McClearn, 1985; Lieber and Blevins, 1989) and non-mammalian (e.g., Willems, 1977; Wineski and Gans, 1984) literature, the functional impact of whole *muscle architecture* on normal behavior has largely been ignored in comparative studies of primate locomotion. How widely disparate architectural variability influences the functional division of labor among the four synergistic bellies

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of quadriceps femoris, however, has been demonstrated in *Lemur fulvus* (Anapol and Jungers, 1986, 1987).

Whole muscle, or fiber, architecture is the three-dimensional arrangement of myofibers with respect to the tendons of origin and insertion. Within a whole muscle, fasciculi (groups of myofibers) are arranged either in parallel or pinnately, i.e., at an angle to a tendon of attachment. Both of these arrangements occur in a wide variety of functionally significant configurations (Gans and Bock, 1965; Gans, 1982; Gans and de Vree, 1989), and may vary greatly, even among the heads of a synergistic muscle group (Anapol and Jungers, 1986). Most studies of muscle architecture focus on the contractile properties of isolated muscles. These electrophysiological studies have established that the arrangement of fibers determines the extent to which a muscle is best suited for force and/or velocity as well as the metabolic expense of whole muscle contraction (e.g., Goslow et al., 1977; Muhl, 1982; Sacks and Roy, 1982; Anapol and Jungers, 1986; Anapol et al., 1987; Anapol and Herring, 1989).

Although relative muscle weights often have been useful in drawing conclusions about behavioral differences [e.g., braking vs. propulsive function (Haxton, 1947); quadrupedalism vs. leaping (Fleagle, 1977)] (Appleton, 1921; Ashton and Oxnard, 1963; Grand, 1967, 1968a,b; Grand and Lorenz, 1968; Stern, 1971; Jenkins and Weijs, 1979; Anapol and Herring, 1989), isolated muscle weight indices (individual muscles as a proportion of some arbitrarily determined standard) are of questionable interpretability (Stern, 1971). Muscle weight is often presumed to approximate force in biomechanical models. The potential force a muscle can generate relative to other muscles, however, differs from its relative weight, and is a function of other variable architectural components. For example, pinnate-fibered muscles enable an increase in the number of cross-bridges in parallel, and can effectively increase total force output and/or concentrate force into a smaller allocated area of attachment. Furthermore, if "developmental constraint" limits the total muscle mass per muscle group of common embryonic origin (Swartz and Tuttle, 1990), alteration of fiber

length and angulation becomes the sole means by which the "division of labor" can be redistributed among bellies of a synergistic group without having to sacrifice the mass of one for that of another. Thus, the permutations available for architectural morphology may illuminate why observed differences in muscle recruitment patterns in homologous muscles of different primates cannot entirely be explained by differences in the gross arrangement of their muscles and positional habits (Jungers et al., 1983).

Muscle fiber architecture is examined in two groups of antigravity muscles—quadriceps femoris (QF) and triceps surae (TS)—in two African guenon species: the semiterrestrial vervet, or green monkey, *Cercopithecus aethiops*, and the arboreal red-tailed monkey, *C. ascanius*. Because QF and TS provide much of the propulsive effort during the support phase of locomotion, these two groups of synergistic muscle bellies were chosen as the potentially most sensitive discriminators between closely related species exploiting slightly different locomotor modalities in the wild. As shown for several primates (e.g., Jungers et al., 1980, 1983; Anapol and Jungers, 1982, 1987) and nonprimate mammals (e.g., Tokuriki, 1973; Rasmussen et al., 1978) through the use of electromyography, the quadriceps femoris extends the leg and the triceps surae extends or plantarflexes the foot just prior to touchdown. Both muscle groups are active throughout support phase to provide a final "push off" at phase termination (ibid.).

To reduce the influence of "phylogenetic noise" (Fleagle, 1979), the most closely related species for which sufficient cadaveric material was available were chosen for study. *C. aethiops* is one of the most terrestrial guenon quadrupeds (Tappen, 1960; Rose, 1974, 1979; Cheney and Seyfarth, 1990), commonly found in woodland savannah throughout sub-Saharan Africa. *C. ascanius* is an arboreal quadruped whose feeding and social behavior has been well studied in the Kibale Forest of Uganda (Struhsaker, 1978; Gebo and Chapman, 1995). As expected, the more terrestrial vervets also are somewhat more sexually dimorphic in body weight (M:F = 1.6:1) than the red-tailed

guenons (1.4:1) (calculated from data in Fleagle, 1988).

Although fundamentally arboreal, *C. aethiops* and *C. ascanius* differ markedly from one another in the percentages of both the kinds of locomotor activities in which they engage and the substrates upon which they spend their time. Vervets spend a large portion ($\approx 20\%$) of their locomotor time on the ground (Rose, 1979). By contrast, red-tailed monkeys rarely have been observed on the ground (in the Kibale Forest) (Gebo and Sargis, 1994). Vervets spend more time walking and running quadrupedally (54% vs. 39%) and less time climbing up and down (30% vs. 43%) than red-tailed monkeys. Both species utilize both horizontal and oblique supports when arboreal, with $< 3\%$ of their time spent on vertical supports for any particular locomotor activity (Rose, 1979; Gebo and Sargis, 1994; Gebo and Chapman, 1995).

Because both *Cercopithecus* species are commonly found negotiating the irregular and spatially disordered arboreal environment, interspecific differences would be predicted to reflect the terrestriality often practiced by vervets. The arboreal environment presents greater complexity and lesser rigidity of supports, tending to favor the "front steering-rear driving" characteristic of primates, as opposed to the "front steering-front driving" of nonprimate mammals (Rollinson and Martin, 1981, after Kimura et al., 1979). Positional behavior on the ground is much less specific in its relationship to the physical characteristics of the environment than in the trees (Rose, 1974). In primates that come to the ground, e.g., *Cercopithecus neglectus*, more walking and galloping (for foraging and alarm/escape, respectively) are observed, with less trotting than arboreal forms (Rollinson and Martin, 1981). Some, including some vervets, practice digitigrady; often, bipedal hops are incorporated into locomotor sequences for visual orientation, or food location, etc. (Rose, 1974). Differences in how semiterrestrial and arboreal primates use their limbs ought to be reflected by differences, not only in their bony morphology (Rodman, 1979; Anapol and Bischoff, 1992; Gebo and Sargis, 1994), but by differences in the architectural

configuration of their constitutive musculature.

A method is also introduced here by which the original resting posture fiber architecture can be reconstructed in cadavers, regardless of limb position during embalming. As a result, specimens previously considered unsuitable for studies of muscle architecture can now provide an abundant resource.

MATERIALS AND METHODS

Six embalmed (in 10% buffered formalin) cadavers of each species were used in this study. Nine cadavers were part of the Neil C. Tappen collection in the Department of Anthropology at the University of Wisconsin—Milwaukee (Tappen, 1991). These were collected in 1957 in Uganda in the Buto and Kibale Forests and in the region surrounding Kampala, and had been formalin fixed soon after death. Three additional vervet cadavers were obtained frozen and were fixed immediately upon thawing: two are from the Barbados Monkey Crop Control Damage Program and one is from the Primate Research Center of Tulane University.

Muscles of both QF and TS were identified in the left hindlimb, following the illustrations and descriptions of Hartman and Strauss (1933), and dissected free from their attachments to bone. Before the muscles were removed, the distances from the proximal tip of the greater trochanter to both the proximal and distal margins of the proximal attachment sites of each of the vasti were measured (using methods adapted from Stern, 1971).

Sampling sites were chosen at normal intersections of longitudinal and transverse planes approximately 1 cm apart. At each site, six neighboring fasciculi were examined by measuring the following: (1) length of fasciculus (l_f) between the proximal myotendinous junction and the distal myotendinous junction; (2) the perpendicular distance (a) from the tendon of insertion to the proximal attachment of the fasciculus; (3) the length of tendon from the proximal attachment to bone to the proximal myotendinous junction (t_p); and (4) the length of tendon from the distal myotendinous junction to the distal attachment to bone (t_d). The sum of (3) and

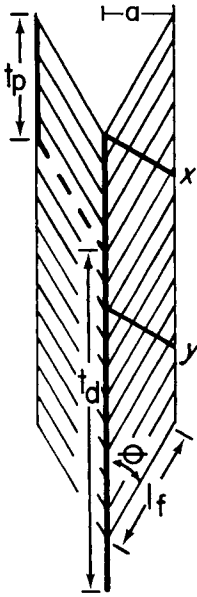


Fig. 1. Diagram of pennate muscle to show measurement protocol of variables; a , distance from proximal myotendinous junction normal to tendon of distal muscle attachment; l_f , length of a muscle fasciculus; t_p , length of the tendon proximal to a fasciculus; t_d , length of the tendon distal to the same fasciculus; x and y (drawn normal to l_f), portions of the true physiological cross-sectional area of the muscle; θ , angle of pinnation (redrawn with alterations from Anapol and Jungers, 1986).

(4) is the total tendon length (l_t) accruing to a muscle fasciculus (Fig. 1).

Finally, the muscles were blotted dry, trimmed of excess tendon and fascia, and weighed. Wet (rather than dry) muscle weights have been commonly used for calculating physiological cross-sectional area (e.g., Spector et al., 1982; Powell et al., 1984; Anapol and Jungers, 1986; Brand et al., 1986). The proportion of weight lost by drying is relatively consistent among muscles, at least for those of the jaws and throat (Schumacher, 1961; Scapino, 1968; Anapol, 1979). Because the reduced physiological cross-sectional area of each muscle is expressed as a proportion of the total of a group of muscles, choice of wet or dry weight matters little, and using wet weight allows preservation of the three-dimensional architecture of the whole muscle, otherwise irretrievably damaged by drying.

Ideally, measurements of fasciculus

lengths and angles of pinnation are accomplished on muscles which are set at *resting length*—the length at which force is of maximum potential. By convention, this is ensured by embalming an unfixed specimen with its legs secured in typical “postural” position as determined through observation of living animals. Unfortunately, most available cadavers (including those examined here) have been embalmed with limbs either flexed or extended so that the muscles are either shortened or stretched relative to resting length. In addition to the effects on fiber lengths, when a pennate muscle contracts or is stretched, the fibers swivel relative to their attached ends, thus altering the angle of pinnation.

To determine resting fasciculus lengths, measured lengths were divided by their percentage difference from resting length. Because resting length could not be determined directly from the available tissue, it was calculated from measurements of A-band length. Isolated myosin is $\approx 1.5 \mu$ and approximates the length of the A-band, while isolated actin filaments are $\approx 1.0 \mu$ in length, and, in resting muscle, overlap 25% of each end of the myosin filament (Huxley, 1957; Ham and Cormack, 1979; Fawcett, 1986). Thus, the theoretical length of a resting sarcomere—the basic contractile unit of a muscle fiber—would be $\approx 2.75 \mu$ and the ratio of A-band length:sarcomere length ≈ 0.55 . Assuming this ratio to be constant, measurable A-band lengths should predict sarcomere lengths because, in vertebrate muscle, thick myosin filaments do not shorten during contraction. Our measurements of visible A-bands (see below) averaged $\approx 1.38 \mu$ and are probably shorter than 1.5μ due to shrinkage and measurement error. This predicts an approximate sarcomere length of 2.5μ , which would be comparable to a preshrinkage sarcomere length of $\approx 2.75 \mu$. Resting length of one sarcomere is thought to be relatively conservative throughout the animal kingdom at approximately 2.5μ (Huxley, 1957) with a range of 2.3 – 2.8μ (Huxley, 1972).

Small ($\approx 2 \text{ mm}^3$) chunks of tissue were removed from proximal, middle, and distal quartiles along the median plane of the length of each whole muscle. Each sample was embedded in paraffin using a vacuum

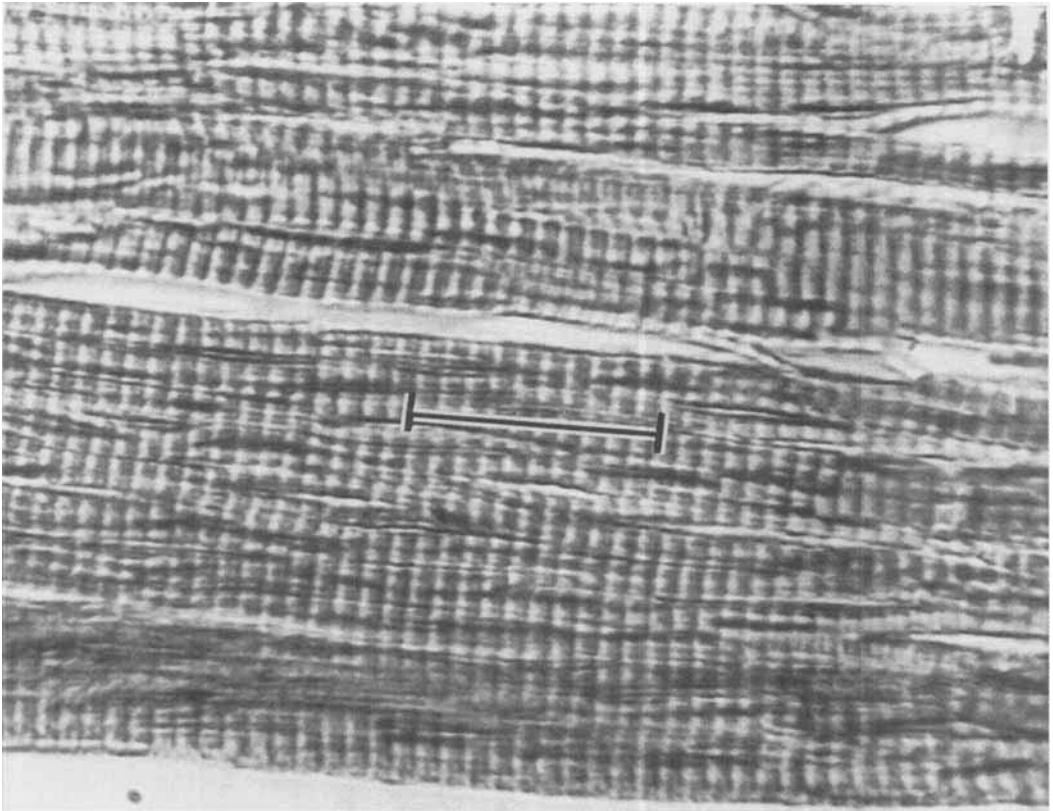


Fig. 2. Videomicrograph of typical serial section ($6\ \mu$ thick) at $400\times$ in bright field. One set of 10 sarcomeres is indicated.

oven [Fisher Isotemp Vacuum Oven 281A; Fisher (Leybold) Maxima D4A Vacuum Pump], serial sectioned at $6\ \mu$, and stained with phosphotungstic acid hematoxylin, following Prophet et al. (1992). Depending on the state of contraction of a muscle fiber at the time of fixation, one or more repeating visible structures—Z (Zwischenscheibe)-lines or discs, A (anisotropic)-bands, or I (isotropic)-bands (Ham and Cormack, 1979)—can be readily identified microscopically with bright field using either $40\times$ and/or $100\times$ (oil-immersion) objectives. The periodicity of whichever of these structures was discernible in any particular sample was used to establish the length of a sarcomere. Videomicrographs were taken with a video copy processor (Mitsubishi P78U) interfaced to a TV monitor (SONY PVM-1341) and a professional video camera (Panasonic Digi-

tal 5010) mounted on a light microscope (Olympus CH2). Staining usually enabled discrimination of banding at the lower power ($400\times$), thus providing more measurements (see below) to be taken per print. When the higher power ($1,000\times$) was needed, prints were made at several loci on the section.

To establish the corrected resting length from measured fasciculus length, lengths of six sets of 10 contiguous sarcomeres in series were measured for each tissue section (Fig. 2). When the muscle shortens or is stretched, the contractile filaments slide past one another, thus altering the length of each sarcomere. To remain as far as possible above the best resolving power ($0.25\ \mu$, Bradbury, 1984; Fawcett, 1986) of the light microscope, the length of a strip of 10 sarcomeres was measured and averaged (Muhl et al., 1978). Thus, the measured length of 10 sarcomeres

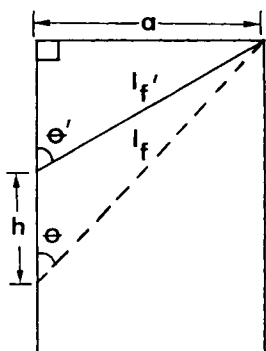


Fig. 3. Diagram showing changes in fiber or fasciculus length and angle of pinnation during contraction. As the tendon of insertion of the whole muscle shortens distance h , the fiber shortens from l_f to l_f' and the angle of pinnation increases from θ to θ' . By measuring a , θ could be calculated after reconstructing l_f from l_f' , as described in Materials and Methods.

(converted to microns), divided by 25.0μ (the presumed length of 10 resting sarcomeres), approximated the percentage difference between measured and resting fasciculus lengths in three regions along the length of the whole muscle. Means of six sets of the sarcomeres were taken to allow for possible uneven contraction throughout a fiber's length.

To correct the angle of pinnation, rather than measure the angle directly, the perpendicular distance from the tendon of insertion to the proximal attachment of the fasciculus was measured (see a , in Fig. 3). Using the calculated resting fiber length, the resting angle of pinnation (θ) was calculated: $\arcsin(a/l_f)$.

From the above measurements, the following variables were computed:

(1) Reduced physiological cross-sectional area (RPCA) was calculated as an estimate of potential force output of each muscle using the formula (Schumacher, 1961, after Weber, 1851, and adjusted by Haxton, 1944): $\text{RPCA (cm}^2\text{)} = [\text{mass (gm)} \times \cos \theta] / [l_f \text{ (cm)} \times \text{specific density}]$, where the specific density of muscle is 1.0564 gm/cm^3 (Murphy and Beardsley, 1974). For each muscle, mean values were used for θ and l_f .

(2) Mass/predicted effective maximal tetanic tension (M/P_0), where $P_0 \approx 2.3 \text{ newtons} \times \text{RPCA}$, was calculated (following Sacks and Roy, 1982) to compare the priority

of force vs. velocity (proportional to fiber length) for any given muscle mass.

(3) Estimated maximum excursion of the distal tendon of attachment (h) was calculated (adapted from Benninghoff and Rollhäuser, 1952) by the equation:

$$h = l_f(\cos \theta - \sqrt{\cos^2 \theta + n^2 - 1}),$$

where n is the coefficient of contraction [(fiber length after contraction)/(resting fiber length)], presumed to be $\approx 70\%$ (Gans and Bock, 1965). For each muscle, mean values were used for θ and l_f . Variable h was normalized for body size differences by dividing by the cube root of muscle mass, thus providing an estimate of whole muscle maximum velocity (\propto excursion/time).

(4) Total tendon length/fasciculus length + tendon length ($l_t/l_f + l_t$) was calculated for each fasciculus to estimate the energy cost of applying force to substrate and the extent to which a muscle might be used *isometrically*, as opposed to *isotonically*. A mean value was determined for each whole muscle.

Means and standard errors were computed for six specimens for each species. In addition, for each architectural variable, the coefficient of variation adjusted for small sample bias (V^*) (Sokal and Rohlf, 1981) was calculated for each muscle group to approximate the extent to which the propulsive effort was divided among muscle synergists. Significant differences were determined by computation of Student's t statistic ($P < 0.05$). Because *percentage* reduced physiological cross-sectional area and tendon length/fasciculus + tendon length are proportions, the raw value for each muscle was arcsin transformed for the statistical analysis (Sokal and Rohlf, 1981). All computations, statistical analyses, and graphs were accomplished using Statistical Analysis System (SAS and SASGraph, SAS Institute, Cary, NC) on a Convex mainframe computer at the University of Wisconsin—Milwaukee.

RESULTS

Gross morphology

The gross morphologies of these two muscle groups are similar in both *Cercopithecus aethiops* and *C. ascanius*. In both guenon

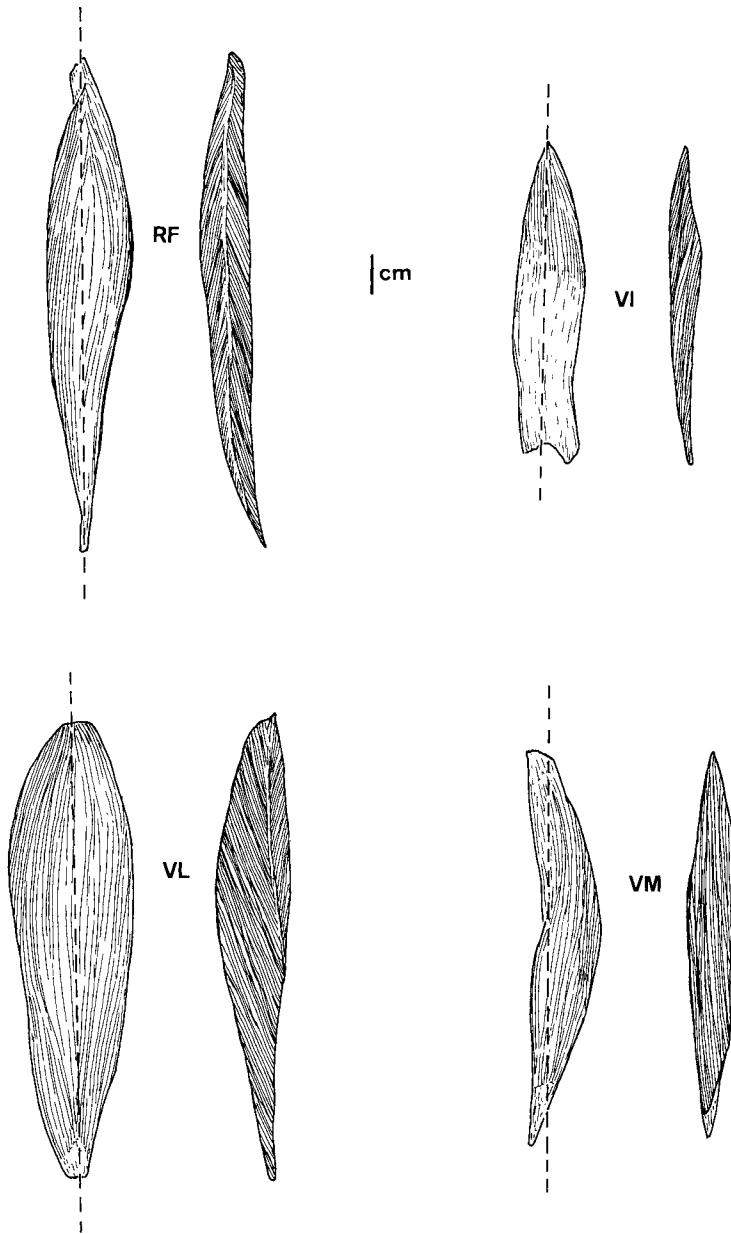


Fig. 4. Superficial aspect (left) and longitudinal sections (right) are provided for representative examples of rectus femoris (RF), vastus intermedius (VI), v. lateralis (VL), and v. medialis (VM) (*Cercopithecus ascanius* shown). Broken line indicates the plane of section of the longitudinal view for which the superficial surface faces left. Proximal is toward the top.

species, seven of the eight muscles exhibited some degree of pinnation with muscle fibers inserting at an angle to the distal tendon of attachment (Figs. 4, 5).

Quadriceps femoris includes rectus femo-

ris (RF) and the vasti peripherales—vastus intermedius (VI), v. lateralis (VL), and v. medialis (VM)—four largely separate bellies located primarily on the anterior aspect of the thigh (Fig. 4). In both species, RF attaches

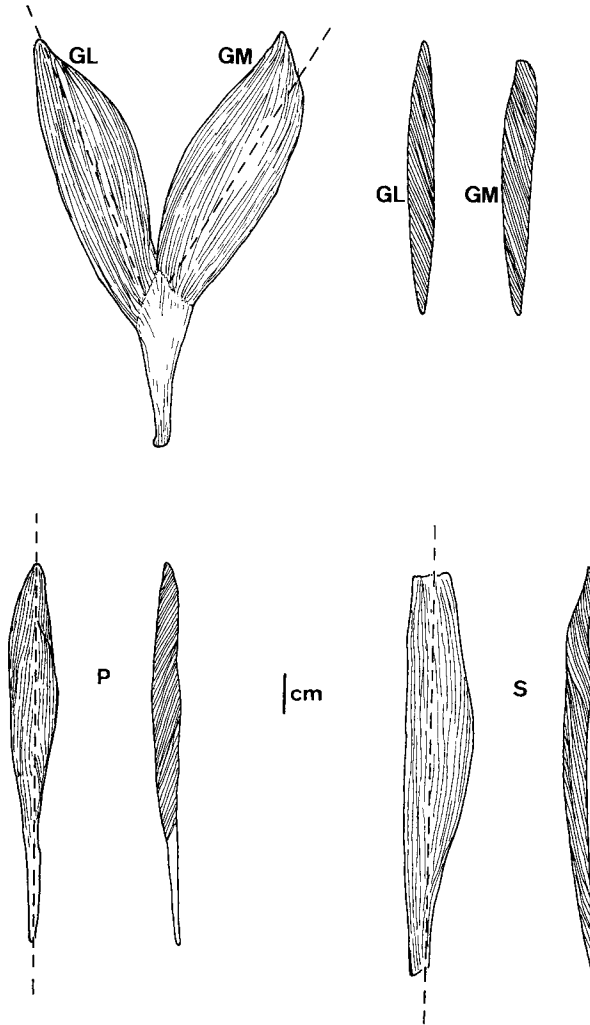


Fig. 5. Same as Figure 4 for gastrocnemius lateralis (GL), g. medialis (GM), plantaris (P), and soleus (S).

proximally via round, thick tendons above the acetabulum. Fiber architecture is most pronounced in RF, a more or less radially pinnate muscle. Fibers arise proximally from a deep central tendon and proceed distally toward a tendinous sheath that surrounds the muscle. The proximal attachment of VI, a unipinnate muscle, is entirely fleshy along the anterior femoral shaft. It is somewhat more extensive in *C. aethiops*, migrating somewhat posterolaterally around the shaft. The proximal attachment of VL is relatively circumscribed on the greater tro-

chanter of the femur. Although basically a unipinnate muscle, in some of the larger specimens, VL shows slight bipinnation toward the distal attachment (e.g., Fig. 4). VM is located on the anteromedial surface of the proximal femur and is parallel fibered in both species. All fasciculi are not equal in length, however, because of the irregular shape of the belly.

All four bellies converge distally, forming the patellar ligament before inserting into the tibial tuberosity. The bellies, especially the vasti, are much more easily separated

TABLE 1. Means (\pm standard error) of distances from the proximal tip of the greater trochanter of the femur to the proximal and distal extents of the proximal attachment sites of the vasti¹

	VI		VL		VM	
	V	R	V	R	V	R
Proximal	0.22 ± 0.05	0.19 ± 0.04	0.06 ± 0.02	0.07 ± 0.02	0.11 ± 0.02	0.13 ± 0.02
Distal	0.83 ± 0.06	0.81 ± 0.08	0.14 ± 0.05	0.13 ± 0.03	0.14 ± 0.02	0.15 ± 0.03

¹V, *Cercopithecus aethiops*; R, *C. ascanius*.

in the more arboreal red-tailed monkeys; in vervets, they are more tightly bound by investing fascia. Immediately before converging to form the quadriceps tendon, the bellies are variably fused, more so in vervets than in red-tailed monkeys.

In Table 1, proximal and distal extents of the proximal muscle attachment of each of the vasti are shown normalized to femur length. Despite some minor biological differences between species, no significant differences were found between mean levels of either proximal or distal extents for any belly. The most dramatic biological difference is that the proximal attachment of VM extends further distally in *C. ascanius* than in *C. aethiops*. Although our measurements are slightly modified from those of Stern (1971) and Kimura et al. (1983), they are nonetheless comparable and most similar to the low values for the arboreal *Macaca fascicularis* (Kimura et al., 1983) and springing/quadrupedal (rather than prehensile-tailed) platyrrhine genera (Stern, 1971).

For this study, triceps surae (TS) is also composed of four bellies, located on the posterior aspect of the crus: gastrocnemius lateralis (GL) and medialis (GM), plantaris (P), and soleus (S) (Fig. 5). In contrast to the slight interspecific differences in VM and VI noted above, the proximal attachment sites are not markedly different between species. The lateral and medial heads of m. gastrocnemius attach proximal to each femoral condyle with a sesamoid bone usually present in the tendon of attachment. Proximally, soleus attaches to the posterior surface of the proximal fibula and the posterolateral surface of the tibia. Distally, GL, GM, and S all converge into the tendo calcaneus (tendo achillis), attaching in common to the calca-

neal tuberosity. Plantaris arises from the posterolateral surface of the distal femur. Its long tendon is located superficial to and separate from the tendo calcaneus, passing beneath the calcaneus to contribute to the plantar aponeurosis.

Architectural morphometrics

Results for six specimens each of *C. aethiops* and *C. ascanius* for reduced physiological cross-sectional area (RPCA), mass/estimated force (M/P_0), estimated maximum excursion of distal tendon of attachment (h), and tendon length/fasciculus + tendon length ($l_f/l_t + l_t$) are presented in Table 2. For almost all variables in both species, the four bellies of the QF are more disparate than the four muscles of the TS. This implies that the labor of propulsion is more divided in the muscles of the anterior thigh than in the posterior crus.

Reduced physiological cross-sectional area. In Table 2, RPCA for each muscle of QF is expressed as a percentage of the combined RPCA of all four bellies of the group. A relatively wide disparity occurs among the four bellies ($V^* = 36.05$ for vervets and 35.69 for red-tailed monkeys), indicating a more pronounced division of labor among muscles in the propulsive effort. The percentage of RPCA ranges from $\approx 10\%$ for VI to $\approx 50\%$ for VL, the potentially strongest muscle of the group. VI is the only muscle in which statistically significant differences ($P < 0.05$) occur between species.

In TS, the constituent bellies are less disparate ($V^* = 20.45$ for vervets and 22.08 for red-tailed monkeys) than those of QF. However, some interspecific differences are present for GL, GM, and S. The percentage RPCA of GL is significantly larger in red-tailed monkeys than in vervets ($P < 0.05$). Percentage RPCA of GM ($P < 0.05$) and S ($P < 0.10$) are both significantly larger in vervets.

Mass/estimated effective tetanic tension. By contrast to the results for RPCA, the values of M/P_0 (Table 2) are less disparate among the four heads of QF ($V^* = 7.61$ for vervets and 8.27 for red-tailed monkeys). Higher values generally indicate longer fibers in vervets, although the interspecific differences are not statistically significant.

TABLE 2. Means (\pm standard error) of calculated variables

	Percentage reduced physiological cross-sectional area		Mass/ P_0		Excursion/ $\sqrt[3]{\text{mass}}$		Tendon length/fasciculus + tendon	
	V	R	V	R	V	R	V	R
Quadriceps femoris								
RF	0.26 ± 0.02	0.27 ± 0.02	1.15 ± 0.17	1.05 ± 0.13	3.81 ± 0.42	3.47 ± 0.40	0.79 ± 0.02	0.81 ± 0.02
VI	0.11 ± 0.01	0.10 ± 0.00	1.32 ± 0.11	1.27 ± 0.18	5.65 ± 0.53	5.43 ± 0.56	0.53 ± 0.03	0.58 ± 0.04
VL	0.49 ± 0.02	0.48 ± 0.02	1.62 ± 0.09	1.52 ± 0.21	3.92 ± 0.22	3.68 ± 0.43	0.65 ± 0.02	0.66 ± 0.02
VM	0.14 ± 0.01	0.15 ± 0.01	1.46 ± 0.10	1.41 ± 0.24	5.44 ± 0.31	5.04 ± 0.57	0.56 ± 0.02	0.57 ± 0.03
Triceps surae								
GL	0.28 ± 0.01	0.35 ± 0.02	1.37 ± 0.18	1.10 ± 0.08	5.48 ± 0.67	4.10 ± 0.26	0.77 ± 0.01	0.80 ± 0.01
GM	0.33 ± 0.02	0.29 ± 0.03	1.32 ± 0.22	1.18 ± 0.17	5.18 ± 0.91	4.60 ± 0.63	0.80 ± 0.03	0.81 ± 0.02
P	0.11 ± 0.00	0.11 ± 0.01	1.12 ± 0.13	0.91 ± 0.09	6.49 ± 0.65	5.37 ± 0.17	0.82 ± 0.01	0.85 ± 0.01
S	0.27 ± 0.02	0.25 ± 0.02	1.28 ± 0.09	0.89 ± 0.11	5.28 ± 0.36	3.91 ± 0.26	0.76 ± 0.01	0.84 ± 0.01

In TS, less intragroup disparity ($V^* = 4.50$) than in QF occurs in vervets but not in red-tailed monkeys ($V^* = 7.40$). Vervets have a significantly ($P < 0.05$) higher ratio of mass to estimated effective tetanic tension in three muscles: GL, P, and S.

Estimated maximum excursion of the distal tendon of attachment. To normalize for differences in body size, and presumed differences in whole muscle weight and fasciculus lengths, h is divided by the cube root of muscle weight (Table 2). In QF, higher disparity ($V^* = 11.01$ for vervets and 11.74 for red-tailed monkeys) is observed among bellies than between species. Slightly higher (but not statistically significant at $P < 0.05$) values are found in vervets than in red-tailed monkeys.

In TS, the bellies are less disparate ($V^* = 5.7$ for vervets and 7.7 for red-tailed monkeys) than in QF. However, significantly greater values ($P < 0.05$) for GL, P, and S are found in the semiterrestrial vervets than in red-tails.

Tendon length/fasciculus + tendon length. In QF (Table 2), again higher variability occurs among muscles ($V^* = 10.0$ for vervets and 8.9 for red-tailed monkeys) for $(l_t/l_f + l_t)$ than between species. The lowest values are found in VI and VM. Although

generally higher values are found in all four muscles in red-tailed monkeys, only that for VI is significantly larger ($P < 0.05$) than in vervets.

In TS, all bellies insert at a more or less common level into tendo calcaneus, resulting in low V^* (≈ 1.7 for vervets; ≈ 1.5 in red-tailed monkeys) for both species. Red-tailed monkeys show significantly ($P < 0.05$) larger values for this variable in GL, P, and S.

DISCUSSION

Differences between the semiterrestrial *Cercopithecus aethiops* and the more committed arborealist, *C. ascanius*, in the physiologically related morphological features of their hindlimb extensors appear to be related to differences in muscle function during positional behavior. Because both species are essentially arboreal, interspecific differences are more likely explicable in terms of the extent to which vervets spend more time on the ground. Two interesting generalities were observed: (1) for each of the variables, the bellies of QF are more different from one another than are those of TS—the labors of locomotion are more clearly divided in the proximal limb segment, while the bellies of the distal segment would appear to function more in cohesion; (2) most of the *interspecific*

differences occurred in TS—differences in locomotor behavior are more clearly reflected by the morphology of the more distal limb segment.

Intersegmental differences in muscle architecture

That a homologous muscle group evolves from a less differentiated mass (Hildebrand, 1974) into more or less separate bellies implies a corresponding partitioning of muscle function to accommodate a more complex and adaptable locomotor modality. That QF was more tightly bound by connective tissue and the vasti somewhat more fused distally in vervets, by comparison to red-tailed monkeys, indicates an adaptive tendency toward *reduced* division of labor for ground quadrupedality. However, for all variables, variation among the bellies of QF (as indicated by V*) was virtually identical between species.

Functional partitioning can be enhanced further through alteration of intramuscular morphology, e.g., fiber architecture or fiber types (Herring et al., 1979; Anapol, 1985; Anapol and Jungers, 1986, 1987). More precise discrimination among constituent bellies resulting from variation in these intramuscular morphological features can significantly extend the behavioral range of a synergistic muscle group. Consequently, the "division of labor" among bellies during locomotion is more pronounced, as documented for QF in *Lemur fulvus* (Anapol and Jungers, 1986, 1987) and TS in both the domestic cat (Walmsley et al., 1978) and *L. fulvus* (Anapol and Jungers, 1982).

The intermuscular diversity present in QF of both of these guenon species may be related to its more proximal limb segment location (therefore, total size of segment controlled) and environmental niche. QF effects movement of and in the entire hindlimb, while stabilizing a relatively unstable (Lachman, 1965) knee joint. Consequently, QF would require more neuromuscular flexibility for control than would TS for a shorter hindlimb segment. Such control must be effected in the precarious three-dimensional arboreal substrate, which is regularly inhabited by both of the species considered here (Jenkins, 1984; Anapol and Jungers, 1986).

Alexander (1974) predicted that, within a

TABLE 3. Mean (\pm standard error) ratio of muscle mass to RPCA (a) QF and (b) TS; mean ratio of total QF to total TS of (c) RPCA and (d) muscle mass

	a	b	c	d
V	3.27 (± 0.19)	2.96 (± 0.31)	2.34 (± 0.31)	2.53 (± 0.16)
R	3.07 (± 0.36)	2.37 (± 0.19)	2.00 (± 0.16)	2.47 (± 0.03)

limb, either parallel-fibered or long-fibered pinnate muscles would be located most proximally and would do substantial work in acceleration and jumping. Short-fibered pinnate muscles would be located more distally and would save energy by elastic storage. In this light, Aerts et al. (1994) suggest that QF performs a power generation and amplification function, while TS is relegated to power transmission. Anatomical and force plate data on standing vertical leaps in *Galago senegalensis* indicate a reliance upon a QF "power amplifier" in which the tendons shorten more rapidly than the contractile fibers themselves (Aerts et al., 1994), e.g., as previously demonstrated by Muhl (1982) in the unipinnate rabbit digastric. Therefore, the extent to which muscle architecture influences muscle function would be indicated by the magnitude of the disparity between the mass of a muscle and its calculated RPCA.

In Table 3, the muscle mass is compared to the calculation of RPCA of both species for total QF and total TS. Because (1) power is a function of distance, and (2) excursion is a function of fiber length and angle of pinnation, the larger values of mass:RPCA (an abbreviated form of M/P_0) indicate longer muscle fibers, hence, greater power. For both species, the higher values are found in QF. However, red-tailed monkeys show a much greater intersegmental difference. Thus, a dichotomy between QF as a "power generator and amplifier" and TS as a "power transmitter" is more pronounced in the more committed arborealist than in the semi-terrestrial vervets. This is further substantiated by comparing the ratio QF:TS for both RPCA and muscle mass (Table 3). In red-tailed monkeys, QF:TS is much greater for muscle mass than for RPCA. This is because of the presence of longer fibers in QF, thus reducing its value for RPCA.

TABLE 4. Relative distribution of variables among constituent muscles of synergistic group (see Discussion)¹

	Percentage RPCA		Mass/P ₀		$h/\sqrt[3]{\text{mass}}$		Tendon length/ fasciculus + tendon	
	V	R	V	R	V	R	V	R
RF	2.4	2.7	1	1	1	1	1.5	1.4
VI	1	1	1.1	1.2	1.5	1.6	1	1
VL	4.5	4.8	1.4	1.4	1	1.1	1.2	1.2
VM	1.3	1.5	1.3	1.3	1.4	1.5	1.1	1
GL	2.5	3.2	1.2	1.2	1.1	1	1	1
GM	3.0	2.6	1.2	1.3	1	1.2	1.1	1
P	1	1	1	1	1.3	1.4	1.1	1.1
S	2.5	2.3	1.1	1	1	1	1	1.1

¹ For each species separately, each value from Table 2 is divided by the lowest value for the muscle group (QF or TS).

Comparable intermuscular morphological heterogeneity among the bellies of QF are found in *Lemur fulvus* (Anapol and Jungers, 1986), an arboreal quadruped that also has a propensity for leaping (Walker, 1979; Tattersall, 1982). Such heterogeneity is considerably more pronounced in the brown lemur than in the domestic cat (Anapol, 1984), a terrestrial quadruped (Leyhausen, 1979). Heterogeneity among the bellies of TS is much less pronounced than in QF for both of these species as well (cat, Sacks and Roy, 1982; *Lemur fulvus*, Anapol, unpublished data). The contrast among bellies of QF in the brown lemur reflects greater functional diversity, as demonstrated by electromyographic recording of muscle activity during normal locomotion (Rasmussen et al., 1978; Jungers et al., 1980; Anapol and Jungers, 1986).

Interspecific differences in muscle architecture

Relative muscle strength. Reduced physiological cross-sectional area predicts the maximum potential force that can be developed by a muscle relative to other muscles. The percentage contribution of RPCA from each belly, relative to the total for a synergistic group, provides an indication of how the potential force is distributed among bellies with respect to normal locomotory function. In comparison to vervets, the distribution of percentage RPCA among the heads of QF in red-tailed monkeys is both more superficial and slightly more lateral (Table 4; Fig. 6). That RF, VL, and VM have greater relative force at the expense of VI suggests

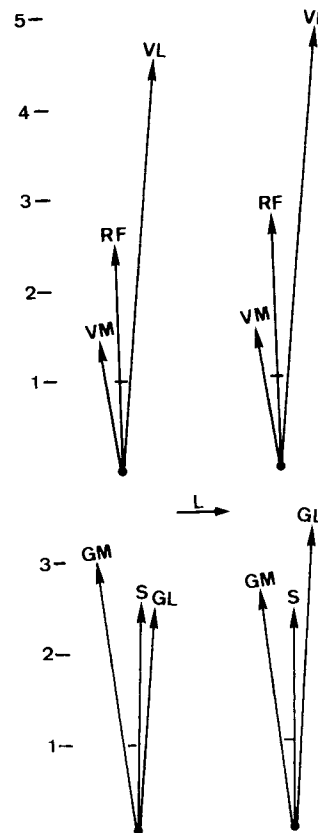


Fig. 6. Arrow directions indicate approximate lines of action for each muscle of quadriceps femoris (top) and triceps surae (bottom) in vervets (left) and red-tailed monkeys (right). Arrow lengths are proportional to percentages of RPCA normalized to VI (—) for QF, and P (also, —) for TS, as found in Table 4. The lines of action are shown viewed along a perpendicular to the femur's long axis, with the horizontal arrow pointing laterally. Abbreviations as in Figures 4 and 5.

increased emphasis on more exertive activities, e.g., leaping and climbing, which incorporate the vertical dimension into the array of demands on positional behavior. A progression from deep to superficial in both inter- and intramuscular force recruitment has been correlated to increasing demands on the locomotor anatomy (Sullivan and Armstrong, 1978; Walmsley et al., 1978; Armstrong, 1980; Jungers et al., 1980; Anapol and Jungers, 1987). The relatively greater increase in VL, compared to VM, in conjunction with similar results for TS (below), suggests that force would be directed somewhat medially, from the lateral side of the thigh (Table 4; Fig. 6). This distribution may indicate a means by which the propulsive effort would be fortified when the supporting substrate is less than body width, as in branch quadrupedalism.

Because of its importance in all locomotor behaviors, i.e., posture, walk/run, galloping, and leaping (Jungers et al., 1980, 1983; Anapol and Jungers, 1987), the larger percentage RPCA value for VI in vervets is correlated either to (1) continual relocation between arboreal and terrestrial habitats, or (2) ground quadrupedalism per se. Were the arboreal-terrestrial transition to require one belly of QF to develop proportionally more strength, a more likely candidate would be VL, which in the brown lemur is a major contributor to high vertical leaping (Jungers et al., 1980). However, in all published mammalian studies, VI is found to be composed primarily of both slow-twitch and fast-twitch high-oxidative fibers (Ariano et al., 1973; Sickles and Pinkstaff, 1981; Anapol and Jungers, 1986). These two classes of muscle fibers are generally thought to bear most of the work during both posture and all *but* the most vigorous of locomotor activities, e.g., high vertical leaping (Walmsley et al., 1978; Anapol and Jungers, 1987). Thus, the somewhat higher force attainable in VI in vervets is more likely due to increased use during ground posture and terrestrial quadrupedal progression.

By contrast to QF, interspecific differences in the distribution of RPCA among the bellies of TS are more dramatically related to locomotor preferences (Table 4; Fig. 6). In red-tailed monkeys, relatively greater po-

tential force is available in GL, compared to GM, while the reverse obtains for vervets. As noted above for QF in red-tailed monkeys, this also indicates a directing of muscle force from the outer, lateral aspect of the leg, inward for branch quadrupedalism. By contrast, both GM *and* the more laterally and deeply situated soleus are relatively stronger in the semiterrestrial vervets. The forces across the span of the ball of the foot are thought to be equally distributed in terrestrial monkeys (Strasser, 1994). Since muscle forces are generally recruited from deep to superficial (Armstrong, 1980), the relatively higher speeds attainable during ground galloping may entail force to be recruited from latero-deep to medio-superficial. This phenomenon may be further effected by digitigrade locomotor posture often used while on the ground by vervets (Rose, 1974).

Relative velocity of contraction. Because all the sarcomeres in a fiber are essentially the same length and contract the same distance more or less simultaneously, relative velocity (distance/time) is proportional to fiber or fasciculus length. Thus, since parallel-fibered muscles generally have longer fibers, they are considered to be an adaptation for speed of contraction, i.e., more sarcomeres in series. A hyperbolic relationship exists, however, between force and velocity, i.e., the higher the load, the slower velocity of contraction (Hill, 1938), a relationship that also extends to pinnate muscles, e.g., rabbit digastric (Anapol et al., 1987).

The calculations of *mass/estimated force* and *estimated maximum excursion of the distal tendon of attachment* both provide some insight into the potential velocity of a whole muscle. The former compares the mass of a muscle with its estimated force output to indicate how much of the mass is due to longer fibers, rather than the number of fibers in parallel. The latter is a direct calculation of how far a whole muscle can contract with regard to the measured length of constituent fasciculi and their respective angles of pinnation. In this study, the results for both variables are comparable.

Like RPCA (above), differences among bellies are greater for QF than TS in both spe-

cies. Thus, the bellies of the more proximal muscle mass are also more individualized in their contribution to the propulsive effort with regard to velocity. The relative distribution of values among bellies is almost identical for both species. The relatively longer fibers in VI (Table 4) in red-tailed monkeys may be required for maintaining muscle length in the plateau region of the length-tension relationship over longer excursions during habitual arboreal climbing (Goslow et al., 1977).

Without exception, all eight muscles are more geared for velocity in vervets, especially in TS where the fibers of GL, P, and S are significantly longer than they are in red-tailed monkeys. Both hip and knee joints may reach flexion and extension more rapidly during ground galloping than during branch quadrupedalism, as previously observed in the brown lemur (Anapol, 1984).

Cost of force transmission and nature of contraction. Each end of a muscle fasciculus attaches either directly to bone or to intervening fibers of tendon. Because tendons are highly resistant to tensile loading, they are well suited for transmitting muscle force to bone. Tendon can be extended reversibly to strains of $\approx 4\%$ (Wainwright et al., 1982); after this small "damping" factor is initially stretched, almost the entire force of the muscle fiber can be transmitted to bone. Since muscle fibers shorten $\approx 30\%$ of their resting length during normal use (Gans and Bock, 1965), having shorter fibers per tendon length will both (1) decrease the expense of force transmission, and (2) enable a muscle to behave more *isometrically* (constant length-changing tension).

During contraction, only the muscle fibers (not the tendon) consume energy by hydrolyzing adenosine triphosphatase (ATP). Thus, replacement of a length of contractile tissue with tendon reduces the expense of contraction without sacrificing tension. When the expense of force transmission is reduced by decreasing the relative proportion of muscle fiber length to tendon fiber length, total excursion is sacrificed. An additional energy savings is possible by using a muscle isometrically because elastic strain energy can be stored in the passive element

and subsequently utilized, e.g., as in human running (reviewed by Cavagna, 1969; Cavagna et al., 1977). In other words, if a muscle and tendon are pulled longer as the force on them increases, elastic strain energy can be stored. Conversely, this energy is returned through elastic recoil by shortening as the force falls. When both events occur during the contact phase of a step cycle, energy is conserved (Alexander and Bennet-Clark, 1977; Biewener et al., 1981). The extent to which the elasticity within the sarcomeres participates in energy storage, however, remains somewhat equivocal (see Cavagna et al., 1980).

Higher values for *tendon length/fasciculus + tendon length* are found in all eight muscles of red-tailed monkeys (especially in VI, GL, P, and S). By contrast to ground running, during a more "bouncing" style of running, as required by the higher compliance of the arboreal substrate (Demes et al., 1994), stretching and immediate shortening of the short fibers would enable a muscle to behave as a passive spring (see Cavagna et al., 1976, 1977; Cavagna and Kaneko, 1977).

The relatively lower values in vervets imply that this semiterrestrial species uses these muscles more *isotonically* (constant tension-changing length) at a relatively greater expenditure of ATP. On the ground, the threat of predators places a higher premium on speed, rather than expense. Longer muscle excursion with more deliberate joint angle changes and foot placement is both less cumbersome and less precarious on the rigid ground than in the more compliant substrate of the trees.

Evolutionary implications

Factors which influence musculoskeletal adaptation to a particular locomotor modality are: skeletal proportions and shapes of bones, level of attachment sites of whole muscles, and muscle morphology, which includes both fiber architecture and histochemical fiber types. However, whether the mechanism by which a species might become adapted to an unaccustomed niche prioritizes one factor or another remains enigmatic.

Because of the frequency and predictability with which it can be linked to locomotor

behavior, skeletal configuration must be the least malleable factor. Regardless of interspecific variation, marked differences in the skeletal postcranial anatomy between closely related species are found to be strongly associated with specific differences in locomotor behaviors (e.g., Jolly, 1972; Fleagle, 1977, 1988; Manaster, 1979; Rodman, 1979; Ward and Sussman, 1979; Schaffler et al., 1985; Fleagle and Meldrum, 1988; Burr et al., 1989; Strasser, 1992).

The level and extent of muscle attachments are also critical to interpreting the mechanics of locomotor adaptation (e.g., Stern, 1971, 1974; Fleagle, 1977; McArdle, 1981). Muscle attachments define the bony lever arm (perpendicular distance from the line of action of the muscle to the joint) and imply significant functional consequences for the force-velocity relationship (Smith and Savage, 1956; Stern, 1974). While muscle tissue itself is capable of transformation (see below) in adjustment to a change of functional requirement within a relatively short time, muscle attachment sites (thus, the mechanical arrangement about the joints) ordinarily do not change within the lifetime of the adult, notwithstanding some functional impairment. In this study, differences in muscle attachment sites between vervets and red-tailed monkeys were not especially illuminating with regard to explaining interspecific locomotor differences.

The most malleable component of the locomotor anatomy is muscle morphology. During a relatively short time span, fiber types can change with training or stimulation (reviewed by Salmons, 1980) and sarcomeres may be added or subtracted to adjust to length requirements (reviewed by Herring et al., 1984). Interspecific differences in muscle architecture and their functional consequences for locomotion have been only briefly touched upon by few investigators, however theoretically. Stern (1971) noted that vasti peripherales in habitually leaping cebid monkeys were characterized by restricted proximal attachments, implying fewer, but longer, muscle fibers. This contrasts to more extensive proximal attachments (more, but shorter fibers) in the relatively nonleaping prehensile-tailed forms. Alteration in pinnation, however, can dra-

matically increase or decrease fiber length (therefore, velocity), without necessarily altering the area of attachment site (Anapol and Jungers, 1986). Thus, despite the overall reciprocity of the force-velocity relationship, altering fiber architecture can either increase the velocity of high-force muscles or increase the force output of high-velocity muscles (see also Stern, 1971).

This apparent greater flexibility in muscle than in bones would seem to enable a species to respond to selective pressure facultatively, while preserving the bony morphology that underlies its more *constitutive* behavior. [*Constitutive* is used here to describe the animal's preferred locomotor behavior, and most closely corresponds to Prost's (1965) "habit types." *Facultative* is used to describe an animal's behavior that can be performed but is not preferred and corresponds to Prost's "totipotentiality" minus "habit types."] As Rose (1974) points out, the mobility of the ateline hindlimb is not only useful in their normal suspensory repertoire but also in their proficient postural and locomotor bipedalism, both in the trees and on the ground. Similar adaptations to climbing behavior have been suggested as preadaptive to human bipedalism (Stern, 1976; Fleagle et al., 1981).

Shape comparisons of the postcranial skeletal elements between *C. aethiops* and *C. ascanius* were previously reported and found to track preferences for locomotor modalities (Anapol and Bischoff, 1992). *C. ascanius* was found to be more closely associated with other arboreal quadrupeds, e.g., *Cebus albifrons*, than was *C. aethiops*. What is especially intriguing, however, is that interspecific differences in the skeletal anatomy were more pronounced (less error-bar overlap) than were the differences in the physiologically related morphological features reported here; i.e., these guenon species are more different from one another in their bones than they are in their muscles.

Thus, the inherent flexibility of muscle permits a greater flexibility in locomotor behavior of a species than that which might be indicated by examination of the skeletal morphology. This flexibility is preadaptive to a shift in behavioral or environmental niche

while allowing functionally significant aspects of the skeleton to evolve more gradually.

CONCLUSIONS

For all variables and for both species considered here, a greater division of labor occurs among the bellies of quadriceps femoris than among those of triceps surae. That the influence of fiber architecture on quadriceps femoris is greater than on triceps surae is consistent with a characterization of the former as a power "generator-amplifier" and the latter as a power "transmitter" (sensu Aerts et al., 1994).

Differences in fiber architecture between semiterrestrial arboreal (*C. aethiops*) and more strictly arboreal (*C. ascanius*) quadrupeds are more prevalent distally in the muscles of triceps surae than in quadriceps femoris.

Interspecific comparisons of physiologically related morphological features indicate: (1) in red-tailed monkeys, the distribution of percentage RPCA is relatively skewed from deep to superficial within quadriceps femoris to accommodate relatively more strenuous locomotor activities, e.g., climbing and leaping; (2) in red-tailed monkeys, the distribution of percentage RPCA is relatively skewed in both quadriceps femoris (slightly) and triceps surae (substantially), such that force would be directed medially, from the lateral side of the limb, for more committed arboreality in which the supporting substrate is less than body width; in vervets, the reverse is true in triceps surae so that force is directed somewhat laterally during ground quadrupedalism; (3) muscle fibers are generally longer in the *C. aethiops*, thus better suited for the increased velocities of ground quadrupedalism; and (4) the muscles of the hindlimb generally are used more isototonically in semiterrestrial species, but relatively isometrically in arboreal species at less expense.

In these two guenon species, interspecific differences in muscle architecture are less pronounced than interspecific difference in shapes of bones. The inherent flexibility of muscle, in allowing a broadened range of locomotor behavior, may be preadaptive to

a shift in behavioral or environmental niche, while allowing biomechanically significant aspects of the skeletal anatomy to evolve.

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